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The effects of vibrotactile masking on heartbeat detection: Evidence that somatosensory mechanoreceptors transduce heartbeat sensations

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Abstract

The ability to detect heartbeat sensations is the most common basis for inferring individual differences in sensitivity to the interoceptive stimuli generated by the visceral activity. While the sensory sources of heartbeat sensations have yet to be identified, there is a growing consensus that visceral sensation, in general, is supported not only by the interoceptive system but also by the somatosensory system, and even by exteroception. The current experiment sought evidence on this issue by exploring the effects of masking the functions of somatosensory Pacinian and non-Pacinian mechanoreceptors on the ability to detect heartbeat sensations. Twelve verified heartbeat detectors completed a multi-session experiment in which they judged heartbeat-tone and light-tone simultaneity under two vibrotactile masking conditions involving the stimulation of the sternum: (a) using 250 Hz vibrotactile stimuli to mask the Pacinian channel, and (b) using 6 Hz vibrotactile stimuli to mask the non-Pacinian channel. A no-vibration control condition in which no masking stimuli were presented was also implemented. Presentation of both the 250 Hz and the 6 Hz masking stimuli impaired the ability to judge the simultaneity of heartbeats and tones but did not influence the ability to judge the simultaneity of stimuli presented to different exteroceptive modalities (lights and tones). Our findings reinforce the view that the somatosensory system is involved in cardioception and support the conclusion that both Pacinian and non-Pacinian somatosensory mechanoreceptors are implicated in heartbeat detection.

KEYWORDS

cardioception, heartbeat detection, interoception, mechanoreceptors, somatosensory pathway

1 | INTRODUCTION

The field of cardioception has received considerable attention from the scientific community for close to fifty years (Brener & Ring, 2016; Jones, 1994). Heartbeat sensations are caused by pulsatile mechanical stimuli generated by ventricular contraction. However, the types of mechanoreceptors and the afferent pathways (interoceptive, somatosensory, exteroceptive) responsible for transducing heartbeat sensations and conveying the information to the brain have yet to be identified. Despite this, measurements of the accuracy of heartbeat detection are the most common means of assessing individual differences in *interoceptive* sensitivity, creating confusion about what is meant by interoception.

Individuals may detect the beating of their hearts through "*the afferent consequences of pulsatile changes on intracardiac mechanoreceptors, on baroreceptors in the aortic arch or carotid body, on mechanoreceptors in the muscles of the thorax, a limb, or a digit, on the auditory receptors via pulsatile actions on the Eustachian Tubes, or on the eyes by watching some part of the body move*" (Brener, 1977, p. 240). This point has been elaborated by others (e.g., Cameron, 2001; Craig, 2003; Khalsa, Rudrauf, Hassanpour et al., 2009) who have provided details of the mechanoreceptors, afferent pathways, and central processes that are implicated in the detection of visceral activity, including the heartbeat. Explorations of this issue have led to a widespread agreement with Khalsa, Rudrauf, Feinstein, and Tranel (2009) characterization of *interoception* as "*afferent information that arises from anywhere and everywhere within the body, including through the skin via pathways that are usually considered to support exteroception*."[1]

In other words, any mechanoreceptors within the sensory range of the pulse pressure wave could detect heartbeat stimuli. This encompasses arterial mechanoreceptors in or near coronary arteries (Brown, 1965), and other interoceptors classified as cardiovascular receptors by Paintal (1972), including carotid, aortic, brachiocephalic and pulmonary baroreceptors, atrial mechanoreceptors, ventricular and epicardial mechanoreceptors and the Pacinian corpuscles, which Paintal classified as pseudo-baroreceptors. Vibrotactile receptors, such as the Pacinian corpuscles, are distributed most prominently in the glabrous skin but are also found in many locations in the body including deep visceral structures[2] and have been shown to fire in synchrony with myocardial contraction. Another ubiquitous class of somatosensory mechanoreceptors that fire in synchrony with heartbeats and that may be involved in the detection of heartbeat sensations are the intrafusal fibers of the striate muscles (Birznieks et al., 2012; see also Watanabe & Hotta, 2017).

One source of experimental evidence which supports the view that heartbeat sensations may be detected through the somatosensory afferent system rather than exclusively through cardiovascular interoceptive pathways comes from studies of heartbeat detection in patients whose interoceptive afferent systems have been compromised. The first experimental study of heartbeat detection in patients with putative damage to the interoceptive cardiac afferent pathway was reported by Pauli and coworkers (1991). They examined cardioception by measuring the accuracy of heartbeat counting in diabetics with autonomic neuropathy, diabetics without autonomic neuropathy, and in healthy controls. Patients with diabetic autonomic neuropathy show faster resting heart rates (Clarke & Ewing, 1982a), reduced spontaneous variation in heart rate (Clarke & Ewing, 1982b), and typically fail to report pain that is usually associated with myocardial ischemia and myocardial infarction (Vinik et al., 1996). These phenomena have been interpreted as evidence that the afferent system which normally conveys information from the heart to the brain has been damaged in individuals suffering from diabetic autonomic neuropathy (Pfeifer & Peterson, 1987). Pauli and colleagues (1991) reasoned that if individuals rely on interoceptive cardiovascular pathways to detect heartbeat sensations, then diabetics with autonomic neuropathy should exhibit impaired heartbeat detection. They tested this hypothesis using a heartbeat counting task (Schandry, 1981), in which the accuracy of heartbeat counting is measured during brief fixed time periods and their expectations were supported by the observation that of the three groups examined in the experiment, diabetics with autonomic neuropathy exhibited the least accurate heartbeat counting.

While these results suggest that the detection of heartbeat sensations is dependent on cardiovascular mechanoreceptors of the interoceptive afferent system, it is unknown whether the diabetics with autonomic neuropathy also suffered from peripheral (i.e., somatosensory) neuropathy. According to Vinik et al. (1996), peripheral and autonomic neuropathies typically co-occur. If the diabetic patients experienced peripheral as well as autonomic neuropathy, then the mechanoreceptors and/or afferent channels used to detect heartbeat sensations cannot be inferred from this study.

Another questionable feature of Pauli and colleagues' inference that patients with diabetic neuropathy have impaired cardioceptive sensitivity concerns the validity of the heartbeat counting task (Schandry, 1981). The validity of this task has been defended recently by Ainley et al. (2020), mainly on the basis of significant correlations between scores on the counting task and behavioral, psychological, and neurophysiological measures (e.g., Fukushima et al., 2011; Mai, Wong, Georgiou, & Pollatos, 2018; Pollatos et al., 2005, 2007, 2016; Tsakiris & Critchley, 2016). However, the construct validity of the counting task has been strongly challenged by experimental studies showing that scores derived from this test reflect the accuracy of the participant's *knowledge and/or beliefs about their pulse frequencies and rhythms* rather than their sensitivity to heartbeat sensations (Brener & Ring, 2016; Corneille et al., 2020; Desmedt et al., 2018; Murphy, Millgate,

[1]Pulsatile tinnitus (Hofmann et al., 2013) in which a discriminable auditory stimulus is generated on each heartbeat and transduced by the auditory channel is an example of how exteroceptive processes could be involved in heartbeat detection. In principle, this product of exteroception should provide sufficient heartbeat information to support good performance on valid tests of cardioceptive accuracy.

[2]Pacinian corpuscles have been found in articular capsules, on tendons and the fascia of muscles, within muscles, near peripheral nerves, near knee joints, in the ureter, female urethra, prostate, urinary bladder, and genital organs of both sexes, in the middle ear cavity and tympanic membrane of the ear canal, in and behind the pancreas and in the neighborhood of the solar plexus and the retroperitoneum, and even on the olfactory bulb (Bell et al., 1994).

et al., 2018; Murphy, Brewer, et al., 2018; Phillips et al., 1999; Ring & Brener, 1996, 2018; Ring, Liu, & Brener, 1994, 2015; Windmann et al., 1999). Therefore, in addition to the likelihood that diabetic patients with autonomic neuropathy also have somatosensory neuropathy, uncertainty about the interpretation of heartbeat counting task scores casts doubt on the validity of Pauli et al.'s (1991) conclusions.

A more direct approach to identifying the contributions of the interoceptive and somatosensory afferent systems to heartbeat detection is to measure heartbeat detection among heart transplant patients in whom the interoceptive pathways conveying information from cardiovascular mechanoreceptors to the brain have been substantially damaged. If heartbeat detection is based primarily on intra-cardiac mechanoreceptors and the associated interoceptive pathway, then by a similar logic to that underlying Pauli et al.'s (1991) experiment, heart transplant patients should exhibit impaired abilities to detect heartbeats.

However, Brener and Ring (1995, p. 205) reported good heartbeat detection in a cardiac patient following heart transplantation, a surgical intervention that interrupts the important interoceptive pathways from the heart to the brain. The patient's ability to detect his heartbeats post-surgically suggests that the somatosensory and/or exteroceptive pathways contributed strongly to cardioception in this patient.

Further evidence that the central ramifications and projections of the somatomotor afferent system are implicated in heartbeat detection comes from a case study by Khalsa, Rudrauf, Hassanpour, et al. (2009) of a neurological patient with extensive damage to the insula and anterior cingulate cortex. That patient's ability to perceive the beating of his heart may be attributed to having an intact bilateral primary somatosensory cortex, adding further support to the hypothesis that heartbeat sensations can be processed by the mechanoreceptors and afferent pathways of the somatosensory system (Hassanpour et al., 2016; Khalsa & Lapidus, 2016).

This hypothesis is congruent with the observations by Barsky and colleagues (1998) regarding the effects of cardiac denervation on heartbeat detection. These researchers asked heart transplant patients to complete a heartbeat detection task (Brener & Kluvitse, 1988) in which participants are required to judge whether heartbeat sensations are simultaneous with tones presented at different time delays (0, 100, 200, 300, 400, 500 ms) following the R-wave of the electrocardiogram. Participants could examine the different R-wave-to-tone intervals for as long and as often as they wished before making a simultaneity judgment. The sensitivity of each experimental participant to heartbeat stimuli was assessed by the chi-square (χ^2) test to compare the *distribution of R-wave-to-Tone Intervals judged to be simultaneous with their heartbeat sensations* to a *rectangular distribution that* would be expected if participants could not detect their heartbeats. If heartbeat sensations are transduced by cardiovascular mechanoreceptors and transmitted to the brain via the interoceptive afferent pathway, then heart transplant patients, who have suffered significant denervation of their hearts (Seifert, 1994), will be less able than normal individuals to detect their heartbeats. However, the study showed that approximately one-third of the transplant recipients could detect their heartbeat sensations, a proportion similar to that in the general population (Brener & Ring, 2016). This suggested that heartbeat detection was not dependent exclusively on intra-cardiac mechanoreceptors and is, therefore, likely to have been supported in these transplant patients by extra-cardiac somatosensory mechanoreceptors stimulated by the pulse pressure wave which traverses the arterial tree on each ventricular contraction.

These results have recently received support from a study by Salamone et al. (2020) of transplant patients whose capacities to detect heartbeat sensations were assessed prior to and following heart transplantation using a novel measure of heartbeat detection (Couto et al., 2014). The accuracy of heartbeat detection had fallen significantly when participants were retested 4 months after heart transplantation but had recovered partially when tested one year following the surgery. This variation in cardioception was attributed to the loss of interoceptive function that resulted from the transplant-related vagotomy but, in agreement with several others (e.g., Cameron, 2001; Craig, 2003; Khalsa et al., 2009; Pollatos et al., 2007), Salamone and colleagues concluded that both the interoceptive and somatosensory pathways contribute to cardioception. However, based on the observation that the participants' intact somatosensory pathways did not compensate fully for the loss in cardioception following vagotomy, Salamone et al. (2020) inferred that the interoceptive pathway is primary.

It has been suggested by some investigators (e.g., Jones, 1994; Khalsa, Rudrauf, & Tranel, 2009; Reed et al., 1990) that the Pacinian corpuscles, a class of rapidly adapting somatosensory mechanoreceptors, may be involved in heartbeat detection. These receptors which were classified as pseudo-baroreceptors by Paintal (1972) have a capsular, lamellar structure that supports very high sensitivity to mechanical stimuli (about 30 times greater than other mechanoreceptors) and have large receptive fields. In humans, they are mostly found on the glabrous skin but are distributed throughout the body (Bell et al., 1994; Sherrick & Cholewiak, 1986). Support for the hypothesis that Pacinian corpuscles may transduce heartbeat stimuli comes from electrophysiological studies showing that Pacinian corpuscles in the cat hind limb and mesentery discharge synchronously with heartbeats (Gammon & Bronk, 1935; Hunt, 1961; Hunt & McIntyre, 1960). Pacinian corpuscles located in the periphery are extremely sensitive to transient mechanical events and produce detectable sensations in response to skin indentations of less than 0.1 microns (Bolanowski et al., 1988;

Gescheider, 1976; Verrillo, 1966a, 1966b). Furthermore, Pacinian corpuscles in the hand and mesentery are physiologically and anatomically similar (Pawson et al., 2009). Therefore, it is plausible that Pacinian corpuscles located in the tissues of the body, and adjacent to blood vessels, are sensitive to the transient mechanical events produced by ventricular contraction.

This possibility was tested here by asking seasoned heartbeat detectors to judge the simultaneity of heartbeats and tones, while being presented with vibrotactile masking stimuli designed to decrease sensitivity to mechanical stimuli in the range of the Pacinian and non-Pacinian mechanoreceptors. *Masking* is defined as a decrease in sensitivity to the test stimulus when another stimulus, the *masker*, is presented concurrently with the test stimulus and to the same sensory channel as the test stimulus (Gescheider et al., 1982). Using the masking paradigm, we examined if heartbeat sensations are detected through the Pacinian channel, non-Pacinian channel, neither of these channels, or both channels (Gescheider et al., 2002, 2004). Masking stimuli were presented to the sternum (breastbone) on the grounds that heartbeat sensations are reported to be located in the chest more than any other site (e.g., Brener & Kluvitse, 1988; Khalsa, Rudrauf, Sandesara, et al., 2009; Ring & Brener, 1992; Salamone et al., 2020).

The Pacinian and non-Pacinian channels are two distinct mechanoreceptor channels that respond to largely different frequency ranges of vibrotactile stimuli and underlie different perceptual functions (Gescheider et al., 2002, 2004). The Pacinian channel is sensitive to high frequency (40–700 Hz) vibrotactile stimuli, with maximal sensitivity at 250 Hz, and mediates the sensation of vibration, whereas the non-Pacinian channel is sensitive to low frequency (2–40 Hz) vibrotactile stimuli and mediates the sensation of flutter (Gescheider et al., 1994, 2004; Verrillo et al., 1983). Therefore, presenting high- and low-frequency vibrotactile stimuli should selectively mask the Pacinian and non-Pacinian channels, respectively.

A methodological issue that needs to be considered is that of inadvertent masking. This can happen in the Pacinian channel when stimuli designed selectively to mask the non-Pacinian channel are presented. Masking in the Pacinian channel has been reported in cases where vibrotactile stimuli are presented near the low-frequency end of the non-Pacinian channel's frequency range (20–40 Hz) at approximately 10 dB above the perceptual threshold (Gescheider et al., 2004). According to Gescheider and colleagues (2004), selective masking of the non-Pacinian channel is accomplished by presenting very low-frequency vibrotactile stimuli, such as 6 Hz, at an intensity high enough to mask the non-Pacinian channel (20 dB above threshold), but clearly well below the intensity needed to stimulate the Pacinian channel (40 dB above threshold). Accordingly, we used a 250 Hz vibrotactile stimulus to mask the Pacinian channel and a 6 Hz vibrotactile stimulus to mask the non-Pacinian channel, with both stimuli presented at 20 dB above each participant's detection thresholds.

If heartbeat sensations are transduced exclusively by the Pacinian channel, then presenting a masking stimulus that preferentially excites the Pacinian channel should impair the ability to detect heartbeat sensations, whereas presenting a masking stimulus that preferentially stimulates the non-Pacinian channel should not impair heartbeat detection. Conversely, if heartbeat sensations are detected exclusively through the non-Pacinian channel, then performance in the heartbeat-tone simultaneity paradigm should be impaired when the non-Pacinian channel is masked but not when the Pacinian channel is masked. However, if both somatosensory channels are implicated in detecting heartbeat sensations, then performance should be impaired when either channel is masked.

Another methodological issue that needs to be considered is that the presentation of vibrotactile masking stimuli could interfere with the general ability to judge stimulus simultaneity. For instance, the masking stimuli may impair performance by interrupting the participant's attention to the demands of the MCS heartbeat detection task which requires judgments of the simultaneity of heartbeats and tones and hence imposes substantial interoceptive and exteroceptive attentional demands. Previous research has shown that the general ability to perceive intermodal stimulus simultaneity as well as the sensitivity to mechanoreceptive stimulation both contribute to heartbeat detection (e.g., Knapp et al., 1997; Ring & Brener, 1992). Accordingly, the non-specific effects of the vibrotactile masking stimuli on the ability to judge stimulus simultaneity were taken into account in this study by examining performance on an exteroceptive-exteroceptive task that required participants to judge the simultaneity of lights and tones. A light-tone task was chosen because it does not involve a mechanoreceptive channel and should, therefore, not be subject to mechanoreceptive masking. If the vibrotactile masking stimuli interfered with judgments of light-tone simultaneity, then impaired heartbeat detection during masking could be attributed to a general distraction or attentional effect. Moreover, if the vibrotactile masking stimuli did not interfere with judgments of light-tone simultaneity, then impaired heartbeat detection could be attributed to a Pacinian and/or non-Pacinian masking effect.

2 | METHOD

2.1 | Participants

Participants were 12 undergraduate students (6 men, 6 women) with a mean age of 26 ($SD = 6.8$) years, a mean weight of 72 ($SD = 19$) kg, and a mean height of 1.67 ($SD = 0.10$). Their average body mass index was 25.49 (SD = 4.93). They were

recruited from a pool of heartbeat detectors ($n = 55$) who were paid $30 and had participated in a previous experiment that employed the Method of Constant Stimuli heartbeat detection task (Brener et al., 1993).

2.2 | Procedure

The experiment comprised three sessions. In the first session, participants completed a standard light-tone simultaneity task followed by a standard Method of Constant Stimuli heartbeat detection task (Brener et al., 1993). At the start of sessions two and three, participants completed a forced-choice adaptive threshold task, in which their detection thresholds for 6 and 250 Hz vibrotactile stimuli to the sternum were determined. In the remainder of sessions two and three, participants judged heartbeat-tone simultaneity or light-tone simultaneity, while being presented with 250 and 6 Hz vibrotactile masking stimuli set to intensities of 20 dB above the participants' detection thresholds. The order of the completion of the heartbeat-tone and light-tone tasks with concurrent vibratory masking stimuli was counterbalanced across participants.

During all experimental tasks, participants lay supine on a padded table in a sound-and-light-attenuated chamber. During the heartbeat-tone simultaneity tasks, the electrocardiogram (EKG) was recorded using the standard lead II electrode configuration. R-waves were identified by a Schmitt trigger that was set to generate a single square wave on each R-wave. A master computer was programmed to present experimental stimuli and to collect trial data. Auditory stimuli (1,000 Hz tones for 10 ms at 75 dB SPL) were presented via a piezo-oscillator situated approximately 2 m above the participant. Sinusoidal vibratory masking stimuli (250 Hz, 6 Hz) were presented to the participants' sternum for 300 ms in the threshold task, and continuously during each trial of the heartbeat-tone task and light-tone task. Visual stimuli (10 ms in light-tone simultaneity task) were presented by the illumination of a light-emitting diode located on a panel situated approximately 2 m above the participant. The light panel consisted of a box measuring 6.35 cm wide by 19.05 cm long on which three light-emitting diodes were mounted (the center light-emitting diode was used to signal the beginning of each trial). Participants held a response box on which two buttons were mounted.

Vibratory stimuli were delivered to the chest by a 2.9 cm^2 contactor activated by a shaker motor (Ling Dynamics Systems, model V102). This assembly was mounted at one end of a 122 cm by 5 cm aluminium beam that balanced on a knife-edge fulcrum; at the other end of the beam, a counterweight compensated for the weight of the shaker motor (650 g). The fulcrum was supported by a tripod that could be adjusted vertically and laterally. During each session that vibrations were presented, the counterweight was adjusted so that the contactor came to rest on the participant's sternum approximately halfway between the manubrium and the xiphoid process with a weight of 50 g. This arrangement minimized variations in the static weight of the contactor on the participant's sternum during movements of the thorax associated with the respiratory cycle.

A separate slave computer controlled the presentation of the vibrotactile stimuli. The sinusoidal output of a function generator was amplified (Hafler Pro 1200 amplifier) and applied to the shaker motor. The displacement of the contactor on the skin was measured by a linear displacement transducer. The transducer's signal was band-pass filtered at the frequency of the vibrotactile stimulus to facilitate removal of variations in transducer output caused by the participant's respiration and heartbeat, and then amplified by an analog transducer amplifier (Lucas Schaevitz, ATA 101). The filtered output from the linear displacement transducer was fed to an analog-to-digital convertor and processed online to provide the displacement measured in microns. During the threshold task, but not during the light-tone or heartbeat-tone tasks, the humming sound produced by the vibrator was masked with white noise (General Radio Company, 1382 Random Noise Generator) that was amplified (Realistic 35 Watt Solid State PA amplifier) and fed to a speaker.

2.2.1 | Light-tone task

In each of the 78 trials, participants were presented with five light-tone pairings at one of the six light-tone stimulus onset asynchronies (−130, −65, 0, 65, 130, 195 ms), and they judged whether or not the tones were simultaneous with the lights. Negative stimulus onset asynchronies indicate that the tones preceded the lights whereas positive stimulus onset asynchronies indicate that tones followed lights. The light-tone pairs were presented every 550 ms. The stimulus onset asynchronies and inter-stimulus interval were chosen for the light-tone task based on past research (Knapp et al., 1997) and the range of stimuli was positively biased because auditory stimuli are processed faster than visual stimuli (see Brener & Ring, 1995). In the present study, a light-tone task of comparable difficulty to the heartbeat detection task was created by reducing the light-tone stimulus onset asynchrony increment from 100 ms (the interval increment on the heartbeat detection task) until the distributions of simultaneity judgments on the light-tone task for the group were not statistically different by chi-square analysis from those exhibited by heartbeat detectors on the heartbeat-tone task (Knapp et al., 1997).

The light-tone stimulus onset asynchrony used on each trial was selected in a quasi-random fashion: stimulus onset asynchronies were presented in an unpredictable order constrained by the requirement that each light-tone stimulus onset

asynchrony occurred an equal number of times. This arrangement meant that participants were exposed to each interval 13 times in the course of the 78 trials, with the stimulus onset asynchronies on each trial being presented in quasi-random, unpredictable order. In each trial, following the presentation of the five light-tone pairs, participants were instructed to press the right button on the response box to register that lights and tones were simultaneous, or to press the left button to register that lights and tones were non-simultaneous. If a button was pressed before the appropriate number of tones for that trial had been presented, an aversive tone was sounded and the trial repeated, otherwise the next trial began 3 s later.

2.2.2 | Heartbeat detection screening task

In each of the 78 trials, participants were presented with five tones at one of the six R-wave-to-tone intervals (0, 100, 200, 300, 400, 500 ms), and judged whether or not the tones were simultaneous with their heartbeat sensations. Following the fifth tone, participants pressed the appropriate button to register their judgment of whether or not the tones were simultaneous with heartbeat sensations. Each interval occurred an equal number of times, with the interval used on each trial determined in a quasi-random fashion as in the light-tone task. This arrangement meant that each R-wave-to-tone interval occurred 13 times in the course of 78 trials. At the end of the session, the participants' performance was evaluated, and only those individuals whose distribution of simultaneity judgments across the six stimulus onset asynchronies differed significantly ($p < .05$) from chance (a rectangular distribution) by χ^2 analysis were classified as heartbeat detectors (Brener et al., 1993) and were asked to return and complete the second and third sessions. The reliability and validity of the heartbeat detection task based on the method of constant stimuli have been established by past studies (e.g., Brener et al., 1993, 1994; Phillips et al., 1999; Ring & Brener, 2018; Schneider et al., 1998).

2.2.3 | Vibrotactile detection threshold task

Two separate blocks of trials were used to determine the sensory detection thresholds for 250 and 6 Hz vibrotactile stimuli. On each trial, participants were presented sequentially with two visual stimuli on the panel located above them; the first stimulus was illuminated for 300 ms on the left-hand side of the display, and following a delay of 620 ms, the second stimulus was illuminated for 300 ms on the right-hand side of the display (Verrillo et al., 1983). On each trial, a vibrotactile stimulus (250 Hz in one series, and 6 Hz in the second series) was presented to the participant's chest, while either the left or right visual stimulus was illuminated. Participants were instructed to press the left button of the response box if vibration was detected, while the left stimulus was illuminated and to press the right button if vibration was felt while the right stimulus was illuminated. The probability of a vibrotactile stimulus occurring during each stimulus was 0.5.

Initially, vibrations were presented at a suprathreshold level (the same level was used for all participants) that had been determined during pilot testing. Following Levitt (1971), two rules were employed to determine the 71% detection threshold. The first rule was that stimulus intensity was reduced by one step following two consecutive correct responses (choosing the interval in which the vibrotactile stimulus was presented). The second rule was that stimulus intensity was increased by one step following an incorrect response (failing to choose the interval in which the vibrotactile stimulus was presented). A variable step size was used. Prior to the first incorrect response, the stimulus intensity was reduced by 1/2 following every second consecutive correct response. Following the 1st, 2nd, 3rd, and 4th incorrect responses, the respective step sizes were 1/3, 1/4, 1/5, and 1/6 of the prevailing stimulus intensity. Thereafter, constant step sizes of 0.33 and 111.60 microns displacement were used, respectively, for the 250 Hz and 6 Hz vibrotactile stimuli. A reversal point was defined as an incorrect response followed by two consecutive correct responses, or two consecutive correct responses followed by an incorrect response. Following the first four adjustments, 10 further reversals were recorded for the task and the detection threshold was estimated by averaging the five ascending and five descending stimulus intensities at these reversal points (the four initial adjustments were not included in calculating the participant's threshold). The sensory detection threshold (dB) was expressed relative to 1 μm peak displacement. Each participant yielded four vibrotactile detection thresholds. The two thresholds for each frequency were averaged to yield one threshold for 250 Hz ($M = 20.82$, $SD = 3.12$ dB) and another threshold for 6 Hz ($M = 38.38$, $SD = 3.21$ dB) vibrations. The intensities of the 250 and 6 Hz masking stimuli (see below) were generated by adding 20 dB to each participant's corresponding sensory detection thresholds.

2.2.4 | Heartbeat-tone task with concurrent vibratory masking stimuli

Participants completed 156 trials of a modified version of the MCS heartbeat detection task, in which they were also presented with a vibrotactile masking stimulus that began at least 1 s prior to the first R-wave-tone pair of each trial and terminated with the last (fifth) tone in the trial. A 250 Hz masking stimulus was used on half of the trials, and a 6 Hz masking stimulus was used on the other half of the trials. The total number of trials was divided into four blocks of 39

trials. During each block, either the 250 Hz high frequency or 6 Hz low-frequency masking stimuli were used and the order of the presentation of the two frequencies was counterbalanced using high-low-low-high and low-high-high-low block designs.

2.2.5 | Light-tone task with concurrent vibratory masking stimuli

Participants completed 156 trials of a modified light-tone task. In this task, concurrent vibrotactile stimuli were presented during each trial (as described above for the adapted version of the heartbeat-tone task).

2.3 | Data reduction and analysis

Separate distributions of simultaneous judgments were constructed for each participant for each of the masking conditions (no vibrations, 250 Hz vibrations, 6 Hz vibrations) associated with the heartbeat-tone and light-tone simultaneity tasks. These distributions were used to calculate interquartile ranges for the different conditions (see Brener et al., 1993). The interquartile range of the distribution of simultaneous heartbeat-tone judgments was used to index the accuracy of heartbeat detection: the greater the accuracy, the smaller the interquartile range. To compare the effects of the vibrotactile masking stimuli on the ability to judge heartbeat-tone simultaneity, a 3 masking condition by 6 interval ANOVA was performed on a square root transformation of the frequency of simultaneous judgments in the heartbeat detection task (see Brener et al., 1993). To further compare the effects of the vibrotactile masking stimuli on the accuracy of detecting the simultaneity of tones and heartbeats a 3 masking condition ANOVA was performed on the interquartile range. Analogous analyses were performed on the data from the familiarization task. A correction (Huynh & Feldt, 1970) was made on all ANOVAs; the original degrees of freedom are reported. We also report the effect size metric, η_p^2 which represents the amount of variance accounted for by the factor(s) in ANOVA, with values of .02, .13, and .25 corresponding to small, medium, and large effects, respectively (Cohen, 1992).

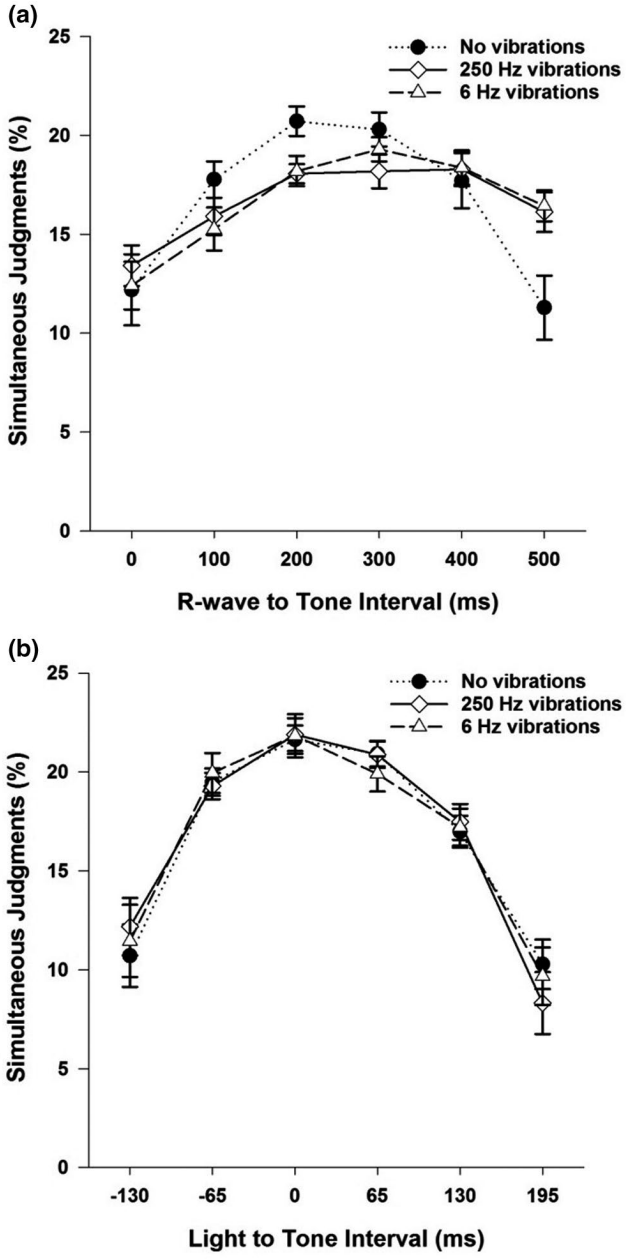

FIGURE 1 The distributions of simultaneous judgments for the heartbeat-tone task (a) and light-tone task (b) under conditions where no vibrations, 250 Hz vibrations, and 6 Hz vibrations were presented

3 | RESULTS

3.1 | Effects of vibratory masking stimuli on judgments of heartbeat-tone simultaneity

The distribution of heartbeat-tone simultaneity judgments in the heartbeat detection task (Figure 1a) was symmetrical with an earlier and more pronounced peak in the no vibration non-masking condition than in either the 250 Hz or 6 Hz vibration masking conditions. A 3 masking condition (no vibrations, 250 Hz vibrations, 6 Hz vibrations) by 6 interval (0, 100, 200, 300, 400, 500 ms) ANOVA confirmed differences between the conditions in the quadratic profiles of the distributions, $F(1, 11) = 16.68$, $p < .001$,$\eta_p^2 = .603$. Specifically, the quadratic distribution of the no mask condition, $F(1, 11) = 22.20$, $p < .001$,$\eta_p^2 = .669$, was more pronounced than those of the 250 Hz, $F(1, 11) = 13.31$, $p = .004$,$\eta_p^2 = .548$, and 6 Hz, $F(1, 11) = 10.59$, $p = .008$,$\eta_p^2 = .491$, masking conditions.

In the heartbeat detection task, cardioception was more accurate with no masking than with masking. A 3 masking condition (no vibrations, 250 Hz vibrations, 6 Hz vibrations) ANOVA confirmed differences between the conditions in the interquartile ranges, $F(2, 22) = 10.22$, $p < .001$,$\eta_p^2 = .482$; the interquartile range was smaller in the no vibration no masking condition ($M = 214.73$, $SD = 27.86$) compared to both the 250 Hz ($M = 253.01$, $SD = 48.09$) and 6 Hz ($M = 246.50$, $SD = 40.64$) vibration masking conditions. The two masking conditions did not differ.

To examine the effects of masking on individual cases of heartbeat detection and non-detection, each participant's distribution of simultaneous judgments in each masking condition was evaluated relative to chance (rectangular distribution) using a χ^2 test (see Brener et al., 1993): a participant was classified as a heartbeat detector if their distribution was non-random ($p < .05$). All participants ($N = 12$, 100%) were heartbeat detectors in the no vibration no masking condition, whereas five (42%) were heartbeat detectors in the 250 Hz masking condition, and only three (25%) were heartbeat detectors in the 6 Hz masking condition.

3.2 | Effects of vibratory masking stimuli on judgments of light-tone simultaneity

In the light-tone task (Figure 1b), the distribution of light-tone simultaneity judgments was symmetrical and similarly concentrated in the three masking conditions. A 3 masking condition (no vibrations, 250 Hz vibrations, 6 Hz vibrations) by 6 interval (−130, −65, 0, 65, 130, 195 ms) ANOVA revealed no differences between the conditions in the quadratic profiles of the distributions of light-tone simultaneity judgments, $F(1, 11) = 0.48$, $p = .505$,$\eta_p^2 = .041$. Specifically, the quadratic distribution was equally peaked for the no masking, $F(1, 11) = 75.74$, $p < .001$,$\eta_p^2 = .873$, 250 Hz masking, $F(1, 11) = 104.33$, $p < .001$,$\eta_p^2 = .905$, and 6 Hz masking, $F(1, 11) = 32.23$, $p < .001$,$\eta_p^2 = .746$, conditions.

In the light-tone task, there were no differences in accuracy of performance between the no-masking and masking conditions. A 3 masking condition (no vibrations, 250 Hz vibrations, 6 Hz vibrations) ANOVA confirmed no condition differences in the interquartile ranges, $F(2, 22) = 0.31$, $p = .737$,$\eta_p^2 = .027$; the interquartile range was the same in no vibration no masking ($M = 134.78$, $SD = 21.50$), 250 Hz vibration masking ($M = 136.72$, $SD = 14.74$) and 6 Hz vibration masking ($M = 138.52$, $SD = 24.09$) conditions.

4 | DISCUSSION

Although the ability to detect heartbeat sensations is the most common basis for inferring individual differences in interoceptive sensitivity or accuracy, there is no direct evidence that performance on tests of heartbeat detection is dependent on the interoceptive afferent system. There is, however, a body of research involving case studies and experiments on cardiac and neurological patients which suggests that the somatosensory system is implicated in the processing of heartbeat sensations (Barksy et al., 1998; Brener & Ring, 1995; Khalsa, Rudrauf, Sandesara, et al., 2009; Salamone et al. 2020). Indeed, the available experimental evidence supports the emerging consensus that cardioception is based on afferent information from the somatosensory system, the interoceptive system, and possibly the exteroceptive system too (Brener, 1977; Cameron, 2001; Craig, 2003; Hassanpour et al., 2016; Khalsa et al., 2008; Khalsa, Rudrauf, & Tranel, 2009; Khalsa, Rudrauf, Sandesara, et al., 2009; Rudrauf et al., 2009).

The results of the current study support the hypothesis that somatosensory afferents fed by the Pacinian and non-Pacinian mechanoreceptors are implicated in the perception of heartbeat sensations. It is inferred that these mechanoreceptors, which are widely distributed in the body, are stimulated by the systolic ejection of blood from the heart and/or the associated arterial pressure pulse wave that is transmitted throughout the circulatory tree.

Adopting a masking paradigm borrowed from vibrotactile psychophysics, the current study found that the application of high-frequency (250 Hz) and low-frequency 6 Hz) vibrotactile stimuli to the sternum impaired the abilities of the majority of intact healthy participants to judge the simultaneity of heartbeats and tones. Importantly, while the masking of Pacinian and/or non-Pacinian somatosensory receptors interfered with heartbeat-tone simultaneity judgment, ANOVA did not reveal any statistically reliable effects of the masking stimuli on judging the simultaneity of lights and tones. These observations support the interpretation that the masking effect on heartbeat-tone simultaneity judgments was not due to a non-specific cognitive interference, such as distracting attention from the task of judging stimulus simultaneity. As such, the findings add support to the view that somatosensory processes contribute to the detection of heartbeat sensations.

Further, while it was found that masking Pacinian and non-Pacinian mechanoreceptors impaired heartbeat detection, ANOVA results indicated that the group as a whole continued to show heartbeat detection during the masking procedure. This suggests that the stimuli responsible for heartbeat sensations, in some participants at least, are derived from sources other than the Pacinian and non-Pacinian channels: maybe involving intra-cardiovascular mechanoreceptors (e.g., carotid baroreceptors, see Edwards et al., 2009; Jennings, 1992) or other somatosensory sources such as the intrafusal fibers of the striate muscles or perhaps even exteroceptive channels such as the auditory stimuli elicited by each heartbeat in pulsatile tinnitus (Hofmann et al., 2013).

An implication of these considerations is that the same heartbeat may generate sensations through several different sensory channels in the same individual and result in a heartbeat perception that is generated by the integration of sensations from these various sources.

Furthermore, the finding that participants varied considerably in their responses to the masking stimuli, provides a reasonable basis for estimating the extent to which the Pacinian and/or non-Pacinian mechanoreceptors contributed to each participant's heartbeat sensations: the more that heartbeat detection declined in the presence of the masker, the greater was the usual contribution of the masked sensory source to the heartbeat sensation. For example, whereas all twelve participants (100%) were heartbeat detectors in the no masking condition, only two of them also qualified as heartbeat detectors under both the 250 Hz (Pacinian) and 6 Hz (non-Pacinian) masking conditions, as identified by the χ^2 criterion described earlier,. Accordingly, it may be inferred that Pacinian and non-Pacinian mechanoreceptors contributed little to the heartbeat sensations of these two participants. Moreover, five participants did not qualify as heartbeat detectors under either the 250 Hz or 6 Hz masking conditions, suggesting that both Pacinian and non-Pacinian mechanoreceptors contributed significantly to those participants' heartbeat sensations. By the same logic, in the four participants who were detectors in the 250 Hz masking condition but not in the 6 Hz condition, it may be inferred that the heartbeat sensation comprised prominent non-Pacinian contributions but negligible Pacinian contributions. The inverse interpretation may be applied to the single participant who was a heartbeat detector in the 6 Hz masking condition but not in the 250 Hz condition.

Our novel findings should be interpreted in light of potential study limitations. First, we only presented masking stimuli to one location: the sternum. Although individuals report detecting heartbeat sensations in their chest more than any other body location, the sensations are felt in other places, such as the neck/head and wrist/hand sites (e.g., Brener & Kluvitse, 1988; Khalsa, Rudrauf, Feinstein, et al., 2009; Khalsa, Rudrauf, & Tranel, 2009; Khalsa, Rudrauf, Sandesara, et al., 2009; Ring & Brener, 1992; Salamone et al., 2020; Yates et al., 1985). Accordingly, in order to define the boundary conditions for the observed heartbeat masking effect, future studies could attempt to extend the current findings by applying masking stimuli to sites other than the chest. The evidence yielded by such a program of research may help to paint a clearer picture of the pathways that mediate normal cardiac sensations.

Second, we presented masking stimuli at only one intensity, namely, 20 dB above the sensory detection threshold. Although this intensity level has been shown to be the minimum intensity required to produce significant masking effects on palmar sites (Verrillo et al., 1983), it is possible that when applied to the sternum, where the density of mechanoreceptors is lower, and this intensity had a different masking effect. This issue could be explored in future parametric studies by using a range of intensities.

Third, we only examined two classes of mechanoreceptors as masking stimuli: Pacinian and non-Pacinian mechanoreceptors. The observation that masking the non-Pacinian channel depressed heartbeat detection at least as much as masking the Pacinian channel was unanticipated and requires further exploration. Individual contributions to heartbeat sensations of other non-Pacinian mechanoreceptive channels (e.g., Merkel discs, Meissner corpuscles, and Ruffini endings) require further investigation, perhaps involving selective masking (Bolanowski et al., 1988). Other mechanoreceptive channels, such as the muscle spindles, which have been shown to respond reliably to the pulsatile stimuli generated by ventricular contraction (Birznieks et al., 2012), should also be examined in this context, as should exteroceptive sources of heartbeat sensations, such as pulsatile tinnitus (Hofmann et al., 2013; Levine et al., 2008).

5 | CONCLUSIONS

The current findings support the view that somatosensory Pacinian and non-Pacinian mechanoreceptors within the receptive range of the sternum contribute substantially to heartbeat sensations. Research is needed to determine the contributions of other mechanoreceptors in the somatosensory, interoceptive, and exteroceptive systems to cardioception among healthy individuals as well as in those with medical conditions. Such research might also examine the extent to which the different mechanoreceptors and sensory systems (interoceptive, exteroceptive, and somatosensory) participate in generating the heartbeat perceptions of particular groups or in different behavioral and psychological states and conditions (e.g., Jameson & Ring, 2000). The masking paradigm employed in the current research may also be applied in studies wishing to assess the effects of reduced cardioception on emotion, cognition, and conation.

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AUTHOR CONTRIBUTION

Kelly Knapp-Kline: Conceptualization; Data curation; Investigation; Resources; Writing-original draft; Writing-review & editing. **Christopher Ring:** Conceptualization; Formal analysis; Methodology; Writing-original draft; Writing-review & editing. **David Emerich:** Formal

analysis; Methodology; Validation. **Jasper Brener:** Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Resources; Software; Supervision; Writing-original draft; Writing-review & editing.

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